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# Eastern Box Turtle (Terrapene C. Carolina) As A Dispersal Vector Of Seeds And Spores

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# THE EASTERN BOX TURTLE (TERRAPENE C. CAROLINA) AS A DISPERSAL VECTOR OF SEEDS AND SPORES

BY

WILLIAM J. JORDAN IV

THESIS

SUBMITTED IN PARTIAL FULFILLMENT OF THE REQUIREMENTS
FOR THE DEGREE OF

MASTER'S OF BIOLOGICAL SCIENCES

IN THE GRADUATE SCHOOL, EASTERN ILLINOIS UNIVERSITY
CHARLESTON, ILLINOIS

2004

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**Acknowledgements:**

I would like to thank the following people for their support in the completion of this project: Dr. Scott Meiners, Dr. Andrew Methven, Dr. Robert Fischer, Drew Foster, Sean Jones, Cathy Jordan, Jenny Foster, Sarah Conrad, Jessica N. Clarke, Emma Greig, Erin E. Barding, Erin Cleere, Susan Linn, Dan Cox, and Dale Waldhoff. I would also like to thank Friends & Co. for supplying libations when they were so desperately needed. Eastern Illinois University and The Lewis Hansford Tiffany Biological Graduate Student Award provided partial funding for this project.

**Abstract:**

Dispersal in highly fragmented landscapes is important in the preservation of natural community structure and in the maintenance of gene flow among isolated populations. Saurochory, the dispersal of seeds via reptiles, and endosaurospory, the dispersal of spores via reptiles, has garnered little attention to date in the field of community ecology. Eastern box turtles (*Terrapene carolina carolina*) are omnivorous terrestrial reptiles found throughout much of the Eastern United States and are known to eat many types of fleshy fruits and fungi, but their ecological role as dispersal agents is largely undocumented. Therefore, the objectives of this study were to: 1) Determine the ecological role of box turtles as agents of seed and spore dispersal; and, 2) Determine temporal patterns of seed and spore dispersal events. Turtles were captured and fecal samples were collected to quantify the number of seeds and spores that pass through the turtle digestive tract. A total of 38 fecal samples were collected between April and September 2003. Of the samples collected, 37% contained seeds. The number of seeds found in samples varied from 1 to 1024 and represented seven different species of plants. The temporal pattern of seed dispersal followed the phenology of fruit availability with the highest amount of seeds dispersed occurred in July. Though turtles do not disperse large quantities of seeds, the quality of turtle seed dispersal may be high relative to bird dispersal due to the selective use of different habitats and deposition of seeds in low-density patches. Spores were found in all fecal samples examined and numbered in the millions per gram of fecal material. Spores were deposited throughout the season and did not vary

temporally. Based on this study, turtles function as seed and spore dispersers and may play an important role in the maintenance of diversity at the population and community level in fragmented ecosystems.

## Introduction:

### *Seed Dispersal in Modern Landscapes:*

Seed dispersal is an important issue for conservationists, naturalists, and ecologists that has not been addressed by the scientific community until relatively recently (Willson 1992). Dispersal determines potential rates of recruitment, range expansion, invasion dynamics, and the genetic structure of plant populations (Loveless and Hamrick 1984, Willson 1992, Pitelka et al. 1997, Brown and Lomolino 1998, Cain et al. 1998, Kalisz et al. 1999, Nathan and Muller-Landau 2000). As populations and communities are often seed limited (Turnbull et al. 2000, Wijdeven and Kuzee 2000), dispersal is also crucial in determining the local abundance of species and community diversity (Augspurger and Kitajima 1992, McClanahan and Wolfe 1993, Jacquemynl et al. 2003). Community assembly and dynamics also are driven by dispersal processes that determine species availability within a site (Del Moral 1998, Mistry 1998, Robinson and Handel 2000, Howe and Miriti 2004). Finally, dispersal may shape the evolution of communities by forming relatively static plant-animal relationships over short time scales (Howe and Primack 1975; Dale 1988).

Dispersal in fragmented landscapes has been shown to play an integral role in forest ecosystem recovery and restoration by supplying seeds for regeneration and community development (McClanahan 1986*a*, 1986*b*, McClanahan and Wolfe 1987, 1993, Augspurger and Kitajima 1992, Robinson and Handel 1993, 2000). For example, recruitment in species dependent on

animal dispersal were 40 times lower in fragmented forests than recruitment in contiguous forests (Howe and Miriti 2004), which suggests that fragmentation may severely disrupt plant/animal interactions. Therefore, the management of plant communities and their respective dispersal vectors can be a useful way to effectively restore functioning communities (McClanahan and Wolfe 1987, Wijdeven and Kuzee 2000, Jacquemynl et al. 2003).

Central Illinois is a prime example of a heavily fragmented landscape where the ability of plants to persist is critically dependent on the dispersal of seeds into suitable habitats. Vectors such as white-tailed deer (*Odocoileus virginianus*) (Velland et al. 2003), birds (Simons and Simons 1993), raccoons (*Procyon lotor*), and coyotes (*Canis latrans*) (Cypher and Cypher 1999) aid in the persistence of plants in fragmented landscapes by dispersing seeds among fragments. The success of species dispersed into patches are subsequently dependent on numerous interactions ranging from mutualistic to antagonistic, such as competition and parasitism (Taneyhill 2000). Summed across multiple species, metapopulation dynamics and the interactions that influence them generate community structure in fragmented landscapes.

While ecological theories often focus on long-distance dispersal events, animals with smaller home ranges and less vagility can also play an important role in seed dispersal (Gervais et al. 1997, Stanley and Lill 2002). Though the volume of seeds dispersed by such vectors may be relatively small, these less-common dispersal agents have the potential to accrue large benefits associated with colonizing new habitats and escaping high levels of density dependent

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mortality. Thus, this thesis focuses on the box turtle as a less common, but potentially important, vector for seeds and fungal spores.

***The Selective Advantage of Seed Dispersal:***

Mechanisms for dispersal are numerous in plants (Howe and Smallwood 1982, Herrera 2002) and fungi, (Gregory 1966, Moore-Landecker 1972, Ingold and Hudson 1993, Deacon 1997) including the evolution of fleshy fruits to entice biotic dispersal and specialized dispersal structures to facilitate transmission via wind and water. While dispersal increases parental fitness and simultaneously increases the survivorship and fecundity of offspring (Willson 1992), the production of specialized dispersal mechanisms is energetically costly (Willson 1993, Hererra 2002) and diverts resources that otherwise would be utilized for growth, storage, and maintenance. Because of the energetic costs associated with dispersal, these mechanisms can only be maintained if there is a selective advantage associated with them.

Among the leading hypotheses that explain selection for and maintenance of specialized adaptations for dispersal are: (1) the escape hypothesis; (2) the colonization or disturbance hypothesis; and, (3) the directed-dispersal hypothesis (Howe 1986). These three hypotheses have been shown to operate in a variety of different systems, are not mutually exclusive, differ in the mechanisms of how dispersal is advantageous, and lead to different predictions of offspring success.

The escape hypothesis describes propagules moving from areas where intraspecific competition with siblings and parents occurs or avoiding high

densities of pathogens or predators associated with the maternal parent. Therefore dispersal results in increased success for seeds and seedlings that escape the vicinity of the maternal plant (Howe and Smallwood 1982, Herrera at al. 1994, Manson et al. 1998, Cypher and Cypher 1999, Packer and Clay 2000, Dyer 2004). Near the maternal plant, competition may be intense for light, nutrients, and space and cause considerable barriers to seedling establishment (Howe and Primack 1975, Howe and Smallwood 1982, Turnbull et al. 2000). In addition, pathogens that infect maternal plants are more easily spread to offspring when they occur in close proximity to one another (Augspurger 1983, Bever et al. 1997, Mills and Bever 1998, Packer and Clay 2000) and insect predation on seeds is often greater beneath the maternal plant than in surrounding areas (Janzen 1970, Connell 1971, Howe and Miriti 2004). Similarly, herbivores and predators often forage preferentially near established plants, which results in increased risk of herbivory and predation for juvenile plants (Janzen 1970, Connell 1971, Manson et al. 1998).

The contribution of dispersal to plant fitness is based not only on the quantity of seeds dispersed, but also on the quality of dispersal (Herrera and Jordano 1981). This includes the condition of the seeds when released from the vector and the quality of the microhabitat to which seeds are dispersed (Jordano and Schupp 2000). As the density of seeds deposited by vectors increases, risk of mortality for seeds and seedlings increases due to density-dependent mortality (Janzen 1970, Connell 1971, Herrera et al. 1994, Manson et al. 1998, Cypher and Cypher 1999, Jordano and Schupp 2000, LoGiudice 2001, Stanley and Lill

2002, LoGiudice and Ostfeld 2002). Therefore, there is an inherent advantage in the dispersal of low densities of seeds to avoid density dependent mortality due to predation, competition and pathogens.

The establishment of new populations and recolonization of previously occupied patches are necessary for the long-term persistence of species in an ecosystem (Taneyhill 2000). The movement of seeds to suitable, uncolonized habitats remote from the parent plant characterizes the colonization or disturbance hypothesis. Dispersal of seeds to uncolonized areas with favorable conditions for germination and establishment benefit offspring by providing new resources for exploitation and allowing for the establishment of new populations (Howe and Smallwood 1982). For example, Stanley and Lill (2002) found that the most common vectors of various fleshy fruits dispersed large numbers of seeds into poor habitats, characterized by high levels of density dependent predation, leading to poor establishment. A small group of relatively infrequent dispersers differed in that they dispersed seeds in low densities to largely unoccupied microhabitats that lead to increased fitness. The colonization of remote habitat patches also increases a species' ability to survive stochastic events and allows for the maintenance of genetic diversity (Nathan and Muller-Landau 2000, Zobel et al. 2000).

The directed-dispersal hypothesis states that vectors disperse seeds to specialized microhabitats that are required for seedlings to develop into adult plants (Howe and Smallwood 1982). An example is the dispersal of the Little Coca (*Erythroxylum ovalifolium,* Erythroxylaceae) by the tree frog *Hyla truncate*

(Hylidae) (Fialho 1990). The frog deposits fecal material in a terrestrial bromeliad, *Neoregelia cruenta,* which holds water year-round and provides the seeds of *E. ovalifolium* with greater survivorship in a moist microclimate (Fialho 1990). Seeds of *E. ovalifolium* dispersed by other vectors tend to be deposited on sandy soils and often die of desiccation (Fialho 1990). Without this directed dispersal, the fitness of *E. ovalifolium* would be greatly reduced.

***The Selective Advantage of Spore Dispersal:***

Dispersal advantages in fungi are analogous to those found in seed dispersal, including: range expansion, population stabilization, and maintenance of genetic variability within populations (Gregory 1966, Ingold and Hudson 1993). Fungi have evolved numerous adaptations for spore dispersal including: 1) ballistic dispersal by coprophilous fungi (Gregory 1966, Deacon 1997); 2) dispersal of self-motile zoospores in water (Gregory 1966); 3) direct release into the environment without ballistic mechanisms (Ingold and Hudson 1993); and 4) adaptations for dispersal by animals (Gregory 1966, Tuno 1999).

Most macrofungi are generally thought of as wind-dispersed (Ingold and Hudson 1993, Tuno 1999) or water-dispersed organisms (Miller et al. 1994). However, endozoospory does occur, and has been documented in a variety of taxa, including flies dispersing the gleba of fungi in the Phallales (Tuno 1998, Tuno 1999), rodents dispersing epigeous and hypogeous fungi (Janos et al. 1995, Reddell et al. 1997, Gordon and Comport 1998, Mangan and Adler 2000,

Mitchell 2001, Pyare and Longland 2001), and Australian marsupials dispersing both epigeous and hypogeous fungi (Johnson 1994, Reddell et al. 1997).

The dispersal of spores via biotic vectors is important in community interactions and may be responsible for providing food sources for soil organisms, increasing nutrient availability, inhibiting soil pathogens and bacteria, facilitating primary succession, and improving soil structure (North et al. 1997, Pyare and Longland 2001). For example, Gehring et al. (2002) found that when terrestrial vertebrates were excluded, the number of mychorrizal spores in the soil decreased significantly. Thus, the lack of adequate spore dispersal can have dramatic effects on community structure and function (Harley 1989, Moore-Landecker 1996, Gehring et al. 2002, Frank et al. 2003). The diversity of a fungal community is also maintained by dispersal events, which may in turn influence the benefits associated with plant-fungal interactions (Baxter and Dighton 2001). Dispersal is not only critical for maintaining the genetic diversity of the community, but is also crucial in the establishment of community interactions over a wide range of taxa (Harnett and Wilson 1999, Castelli and Casper 2003). Similar to seed dispersal, many factors influence spore germination after dispersal, such as the probability of being deposited in suitable habitats, nutritional availability, and the probability of encountering appropriate genotypes of spores to induce reproduction and growth (Tuno 1999).

***The Eastern Box Turtle as a Dispersal Vector:***

One facultative frugivore/mycovore, which may play a role in seed and spore dispersal, is the eastern box turtle (*Terrapene carolina carolina*). In general, very little attention has been given to saurochory, the dispersal of seeds via reptiles (Traveset 1998, Liu et al. 2004). Saurochory has been described for several lizard species: *Teius teyou* (Varela and Bucher 2002) *Gallotia galloti* (Valido and Nogales 1994), *Iguana iguana* and *Ctenosaura pectinata (*Benitez-Malvido et al. 2003) as well as nine species of terrestrial turtles including three that are native to North America: the Texas tortoise (*Gopherus berlandieri*) the desert tortoise (*Gopherus agassizii*), and the eastern box turtle (Moll and Jansen 1995).

The distribution of the eastern box turtle ranges from Massachusetts to Georgia and west to Michigan, Illinois and Tennessee (Conant and Collins 1998). Box turtles are opportunistic omnivores that consume a variety of food items including annelids, mollusks, insects, amphibians, small mammals, carrion, fungi, and plants (Ernst et al. 1994, Dodd 2001, Liu et al. 2004). Plant materials consumed by box turtles include a mixture of roots, stems, leaves, and fruits. In laboratory settings, box turtles have been shown to consume a variety of fleshy fruits and pass viable seeds through their digestive tract (Braun and Brooks 1986). Despite these studies, very little information has been gathered on the ecological significance of box turtles as seed dispersal vectors in natural systems (Liu et al. 2004).

While the potential for box turtles to be effective dispersers has been demonstrated, the frequency of dispersal events in nature is essentially unknown in many fragmented landscapes, such as the Midwest. Box turtles, like numerous other dispersal vectors, alter seeds through scarification and removal of fruit pulp, and gut passage often leads to enhanced seed germination. Braun and Brooks (1986) reported that the seeds of five species of plants germinated at higher percentages after passing through the gut of a box turtle. Liu et al. (2004) found that seed germination in *Serenoa repens* was greatly enhanced after passing through the box turtle digestive system while Rust and Roth (1981) found that the seeds of *Podophyllum peltatum* (mayapple) had a shorter germination period following defecation by box turtles.

Turtles also actively feed on the sporocarps of the Basidiomycota and Ascomycota, and incidentally ingest large numbers of fungal spores when feeding on other food items. Yeasts typically occur on fruits that turtles consume, and soil fungi can be ingested when turtles feed on snails, slugs, vegetation, and carrion. The phenomenon of incidental spore ingestion and subsequent dispersal has been documented in birds (Cafarchia et al. 2002) and may represent an uncommon, but important dispersal pathway. Though reptilian endozoospory has not been previously documented, box turtles may serve as important spore vectors.

Seed and spore dispersal is linked inherently with the movement and behavior of vectors. Movement determines the spatial and temporal distribution of seeds and spores across a landscape and should be considered when

determining the dispersal importance of a vector. Box turtles have been shown to move widely within their home ranges (Stickel 1950, Dodd 2001). The average distance a box turtle moves in one day is approximately 50 m, but they often return to their form (sleeping site) at the end of the day (Stickel 1950, Strang 1993). The paths turtles traverse vary greatly with moisture, temperature, and humidity (Stickel 1950, Claussen et al. 2002, Dodd 2001), leading to variation in habitat utilization. Because the distances box turtles move are appreciable, and their gut retention times range in the time span of days, they are potentially important dispersal vectors (Braun and Brooks 1986).

To date little information exists on the ecological significance of box turtles as dispersal vectors, especially in highly fragmented ecosystems. Thus, I choose to investigate the ability of box turtles to act as seed and spore vectors in the highly fragmented ecosystems of central Illinois by capturing wild turtles and collecting fecal samples to address the following questions: 1) What is the abundance of seeds in fecal samples of the eastern box turtle?; 2) What plant species are being dispersed by turtles?; 3) What is the abundance of spores in fecal samples of the eastern box turtle?; and, 4) Do seasonal variations occur in seed and spore dispersal?

**Methodology:**

This study was conducted in Clark, Clay, Coles, Moultrie, and Shelby counties in east-central Illinois. Turtles were collected by visually scanning the forest floor and roadways from April to September 2003. During collection periods, the abundance and identity of fruiting plants potentially consumed by eastern box turtles were noted. Once observed, turtles were hand captured and transported to Eastern Illinois University. For each turtle, the sex, carapace length, plastron length, and approximate ages based on ring counts of the carapace were recorded. Though the ring count method does not accurately represent the exact age of a turtle, it is a reasonable assessment of age groups, e.g., mature or immature (Wilson et al. 2003). Turtles were placed in 5-gallon buckets for a period of up to three days to allow time for the turtles to defecate. Turtles were released at the point of capture once the turtle had defecated or at the end of the three-day period. Fecal samples were removed from the buckets and immediately placed in a drying oven at 23°C until dry. All samples were then stored at 5°C until analyzed for seeds or spores.

***Quantification of Plant Propagules:***

A mortar and pestle was used to break dried fecal samples into finer pieces. Processed samples were examined under a dissecting microscope (Olympus SZX12) with a magnification range of 7-90X. Seeds were separated into storage vials based on seed morphology. Seeds collected from samples

were identified to species using reference collections of Eastern Illinois University or a field guide (Schopmeyer 1971).

***Quantification of Fungal Spores:***

Spore enumeration techniques were adapted from Gordon and Comport (1998). A homogeneous 0.25g sub-sample of each fecal sample was diluted to concentrations of 1:20, 1:1,000, and 1:10,000. Samples from each dilution were examined using a haemocytometer counting chamber to quantify spore density and spores per gram of fecal material. Cotton blue was used in the 1:1,000 dilutions to facilitate examination of spores in the viewing area. All samples were examined for fungal spores except for the April sample, which did not contain sufficient material for analysis.

***Statistical Analyses:***

Because of the non-normal distribution of data collected, distribution free nonparametric statistics were used in all analyses. Monthly variations in spore and seed abundances were analyzed with a Kruskal-Wallis Test. The month of April was dropped from this analysis as it contained only one fecal sample. Data from August and September were combined to increase replication late in the season. To analyze male/female differences in the number of spores and seeds dispersed, a two-sample Kolmogorov-Smirnov test was used. Nonparametric Spearman rank-sum correlation was used to determine if an association existed between ring count (a surrogate of turtle age) and spore and seed abundances.

All analyses were conducted using SPSS 12.0 for Windows (SPSS Inc., Chicago, IL). A p value of 0.05 was determined to be significant in all tests.

**Results:**

A total of 38 individuals were captured and produced fecal samples. Over twice as many females (25) were collected than males (13) (Fig.1). This sex bias was particularly obvious early in the season. In the month of May, 12 females were found and only two males were located. Although this disparity existed no significant difference was found in seed dispersal (Kolmogorov-Smirnov Z= 0.569, p=0.902). or spore dispersal (Kolmogorov-Smirnov Z= 1.110, p=0.163) based on sex. In addition, there was no correlation found between carapace size and spore abundance (Spearman Rank-Sum correlation r=-0.026, p=0.884) and seed (r=-0.031, p=0.855) dispersal. Like wise no correlation was found between plastron size and spore (r=0.104, p=0.553) and seed (r=0.043, p=0.803) density, a weak correlation existed between the number of rings counted and seed dispersal (r=0.330, p=0.046) assuming ring counts give some broad level information on age.

Of the 38 samples collected, 37% where found to contain seeds, and a total of 2,457 seeds recorded from seven plant species (Table 1). The largest quantity of seeds for an individual sample was 1,024 while the lowest quantity for an individual sample was 1. Through field observations of available fruit, and subsequent examination of fecal samples, *Rubus spp.* is believed to contain both *Rubus allegheniensis* and *Rubus occidentalis*. However, it appears that only a single species was present in the individual samples as seeds of equal size were found in a give sample at a time, and size is the determining factor in differentiating the two species. Although nearly all seeds recovered were

rosaceous plants seeds were also recovered from a legume and a grass. One relatively large underdeveloped seed was recovered that could not be identified.

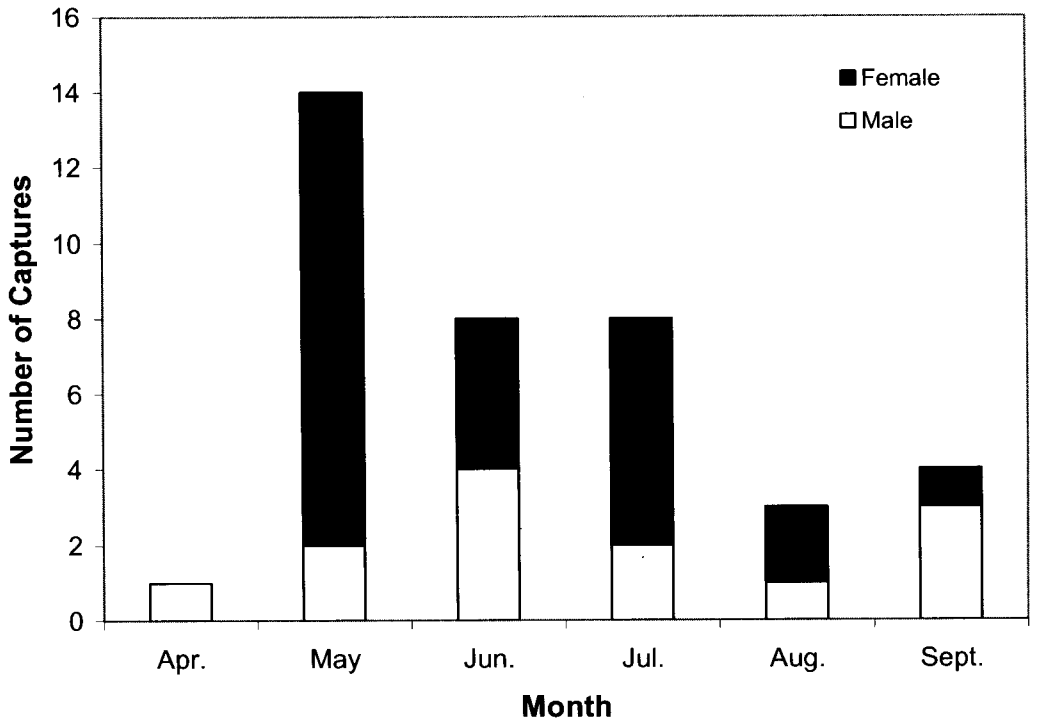


Figure 1. Temporal pattern of turtle captures.

Table 1. Quantification of seeds and the taxonomic groups represented in samples.

| Species | Family | Count | % of total |
|---|---|---|---|
| *Rubus spp.* | Rosaceae | 2,324 | 94.59 |
| *Fragaria virginiana* | Rosaceae | 124 | 5.05 |
| *Prunus serotina* | Rosaceae | 5 | 0.20 |
| *Trifolium repens* | Fabaceae | 2 | 0.08 |
| *Glyceria striata* | Poaceae | 1 | 0.04 |
| Unknown | NA | 1 | 0.04 |

Fecal samples also contained snail shells, insect parts (legs, heads, and elytra), soil, wood, and, in one sample, mammalian remains (fur and two small bones).

Seeds were recovered from fecal samples collected from May through August (Fig. 2) and varied significantly among months. There was a gradual increase in the number of seeds found from April to June with the largest number of seeds being collected in July (Kruskal-Wallis test: $\chi^2$=15.044, df=3, p=0.002). The pattern of seeds found matched that of fruit availability. All seeds found typically ripen in early to late summer. No spring ephemerals were found in the samples, and no samples contained multiple species of seeds.

Fungal spores were found in 36 of 36 (100%) fecal samples analyzed. The 1:1,000 dilutions were most appropriate for counting spores. The 1:20 dilutions contained clumped debris, which made accurate enumeration difficult, while the 1:10,000 dilutions contained too few spores to give reliable counts. The number of spores recovered was calculated to range from 26 million to 226 million per gram of fecal material (Fig. 3) but did not vary significantly across time (Kruskal-Wallis test: $\chi^2$=6.288, df=3, p=0.098). The sample from April did not contain spores. While fungal identification is ongoing, fungi from the Divisions Deuteromycota, Zygomycota, and Basidiomycota have been identified thus far.

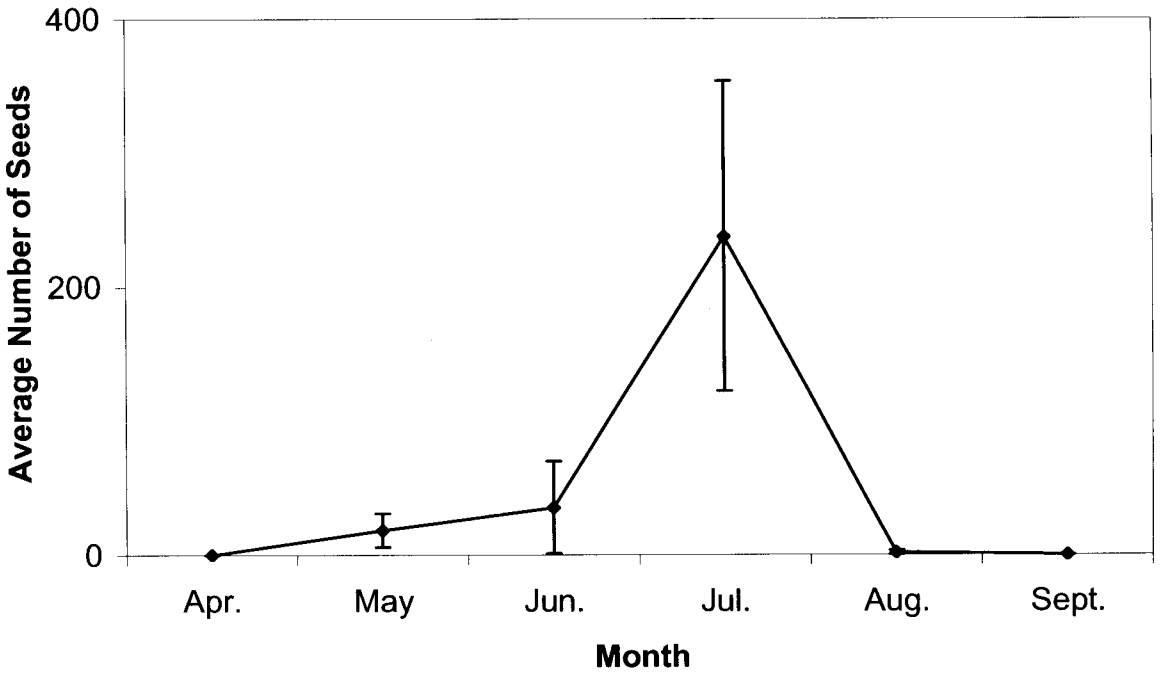


Figure 2. Temporal pattern of seeds found in turtle fecal samples by month. Data presented are means ±1 SE.

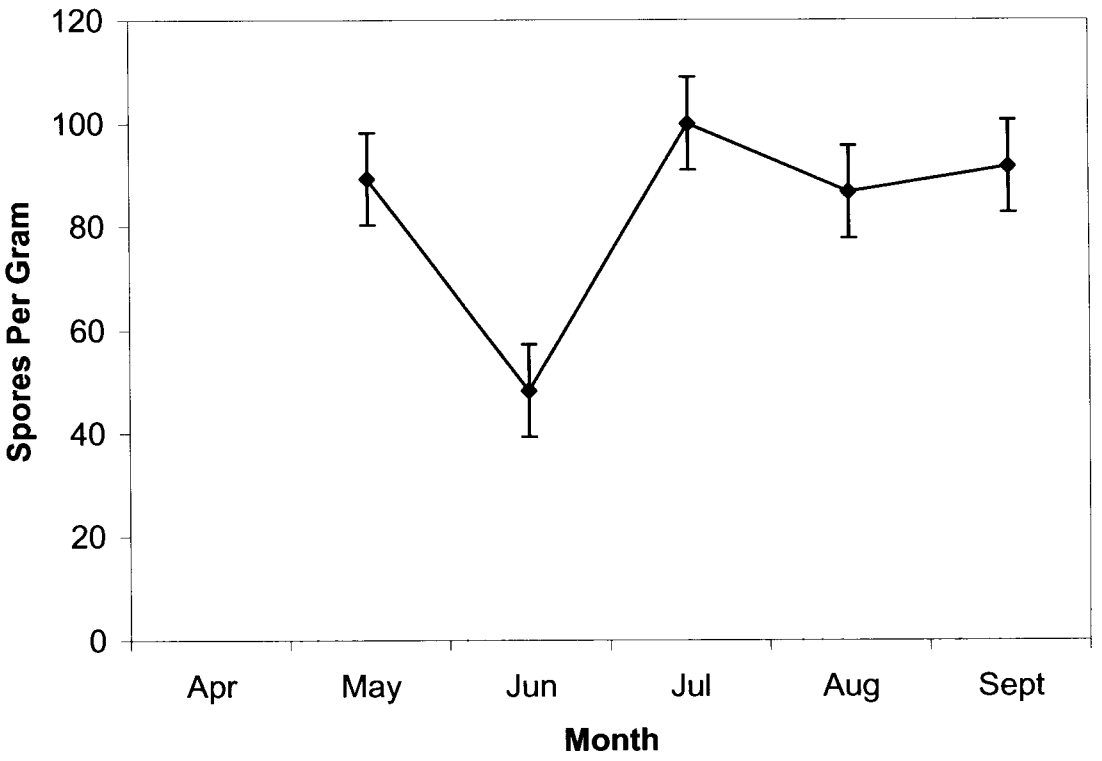


Figure 3. Seasonal distribution of spores. Average number of spores per gram of fecal matter in millions. Data presented are means ±1 SE.

## Discussion:

### *Turtle dispersal of seeds:*

Box turtles were found to disperse seeds of seven plant taxa in central Illinois. Of the fleshy-fruited seeds collected, all were in the family Rosaceae and included the vast majority of seeds recovered. The most abundant members of the family found were *Rubus allegheniensis* and *Rubus occidentalis*. Other members of the Rosaceae represented were *Fragaria virginiana* and *Prunus serotina*, respectively. Based on this data it appears that eastern box turtles may be important dispersers for these species.

An important factor when considering the relative significance of turtle dispersal, at least in *Rubus* and *Prunus*, is that these seeds would not otherwise have been dispersed. Turtles would not have access to these fruits until they fall from the plant. Without secondary dispersal, these seeds and the resulting seedlings would experience all of the negative impacts associated with high densities (Jordano and Schupp 2000, Packer and Clay 2000). Since gut passage through turtles often enhances germination similar to gut passage by birds (Braun and Brooks 1986, Liu et al. 2004). Secondary dispersal by turtles may provide a reliable backup to avian dispersal.

Nonfleshy fruits were also found in the fecal samples. These seeds were probably ingested incidentally while feeding on other vegetative matter as there are no disperser rewards (e.g., nutritive tissues) for consuming these fruits. The potential exists for infrequent but important dispersal events for nonfleshy plant species. These species, with otherwise poor dispersal abilities, may be moved

quite large distances (Quinn et al. 1994) when accidentally ingested by turtle species during feeding.

The temporal pattern of seed dispersal followed the phenology of fruit availability. *Fragaria* was generally found earlier in the season, *Rubus spp.* were found shortly after, followed by *Prunus*. Fruits of *F. virginiana* generally ripen in late Spring and early Summer, *Rubus spp.* in July and August, and *P. serotina* in mid to late summer. There was a peak in the number of seeds dispersed in July (largely *Rubus spp.*), apparently correlated with the increase in the number of ripe fruit available to box turtles. No samples contained multiple species of seeds. Because fruit ripening overlapped, dispersal of mixed species pools would be expected. This disparity between fruit availability and consumption pattern may be caused by limited availability of fruiting plant species within the home range of the turtle or individual food preferences of the turtles.

Turtles have been shown to be largely carnivorous when young and become increasingly omnivorous as they age (Ernst and Barbour 1972). An increase in omnivory could be attributed to learning when and where fruits are available in their home range. This would provide reliable and easily located meals as opposed to hunting, capturing, and handling mobile prey items. Evidence for this diet shift was observed based on a correlation between ring counts and seed abundance. However, other measures of turtle age, including plastron and carapace size, were not correlated with seed abundance. Turtles captured in this study may have learned where to locate fruits over the span of their lifetime and show site fidelity by foraging within a particular area when the

fruits of one plant species become available. However, without direct correlations between seed abundance and other morphometrics more evidence is needed to truly conclude learning is occurring.

There was a complete lack of spring ephemerals in the samples collected, though these species are known to be eaten by box turtles. The seeds of jack-in-the-pulpit (*Arisaema triphyllum*) and mayapple (*Podophyllum peltatum*) passed through the digestive system in Brooks and Braun (1987), and germinated at significantly higher rates when passed. Rust and Roth (1981) also found that the seeds of *P. peltatum* had a shorter germination period when passed through a box turtle gut. *Arisaema triphyllum* and *P. peltatum* were abundant in all sites where turtles were collected (personal observation). The availability of these species across study sites suggests that lack of availability was not the cause of their absence in turtle diets. Perhaps these food items were not preferable to box turtles when other options existed because of dietary requirements or feeding preferences such as taste, smell, and accessibility.

The spatial pattern of dispersed seeds by turtles is very different from that of avian dispersers and potentially makes turtle dispersal a higher quality event. Though they are often considered long distance dispersal vectors, birds deposit seeds in a clumped fashion, (McDonnell 1986, McClanahan and Wolfe 1993, Robinson, and Handel 1993). This patchy dispersal pattern is related to the presence and distribution of perch sites within the habitat (McDonnell and Stiles 1983, McDonnell 1986, McClanahan and Wolfe 1987, McClanahan and Wolfe 1993, Robinson and Handel 1993). Densities of seeds deposited under perching

sites are typically much higher than densities associated with turtle dispersal events. While turtles would disperse individual clumps of seeds as they move, there would not be an accumulation of seeds over time as seen in birds. The high density of seeds under avian perch sites may also lead to increased predator densities (Janzen 1970, Jordano and Schupp 2000) and competition (Cheplick 1992, Cheplick 1993, Cypher and Cypher 1999, Traveset et al. 2001). While turtles surely disperse numerically fewer seeds than birds, they may be more effective than birds at dispersing seeds that successfully germinate and become established based on the risks that coincide with high seed densities.

Though the taxa of seed species dispersed by turtles are not unique, turtle dispersal may offer advantages based on the ability of turtles to disperse seeds into forest interiors. McClanahan and Wolfe (1993) showed that birds are limited in space by the presence or absence of perches. Similarly, Erdelen (1984) found that relatively few bird taxa would go beyond forest edges and penetrate the forest interior. Though, birds and turtles consume many of the same fruits, turtles may disperse seeds to habitats largely ignored by birds. Dispersal into uncolonized habitats increases the quality component of dispersal if these habitats supply adequate resources for exploitation (Jordano and Schupp 2000). A comparison of the relative advantages and disadvantages of individual dispersal vectors and their respective impacts on population dynamics would be highly useful in community ecology.

Through the evaluation of turtle diet and observations made on the habitat structure of the study areas, seeds dispersed by eastern box turtles potentially

benefit through predictions made by both the escape and colonization hypotheses. Not only do seeds escape the density dependent cost of occurring in high densities (escape hypothesis), they also are aided in potentially establishing new populations in otherwise uncolonized areas of the habitat (colonization hypothesis). To a lesser extent, box turtles may aid in distributing seeds in microhabitats that are potentially beneficial to the seeds being dispersed. The selection for and maintenance of specialized adaptations for dispersal may facilitated by eastern box turtles and other generalist frugivores.

***Turtle Dispersal of Spores:***

Spores were found to be extremely abundant throughout all samples. These data show a great potential for dispersal via box turtles as they probably disperse spores in a very different manner than typical vectors. The spatial pattern of turtle dispersal concentrates spores together where they would otherwise be dispersed randomly via abiotic factors such as wind and water. Spore dispersal is highly variable based on climactic conditions and morphology, and dispersal distances can vary from several meters to thousands of meters (Ingold and Hudson 1993). Turtles may increase the quality component of dispersal by defecating large numbers of spores within their home ranges, which may facilitate growth and reproduction of the fungi. Wind and water dispersal may disperse many propagules to poor quality habitats or even outside of the habitat patch. Overall, turtles may function to deposit spores in a similar manner to other terrestrial vertebrates.

**Conclusion:**

Box turtles show great potential for dispersing seeds and spores. The quantity of seeds dispersed by box turtles is appreciably lower than the quantity that birds disperse. However, there is the potential for an increase in the quality of dispersal based on the low densities of seeds deposited and the exploitation of different habitats. This is the first time box turtles have been documented in dispersing fungal propagules. They dispersed large quantities of spores and must be considered important fungal spore dispersers within fragmented landscapes. Though not numerically the most important dispersal vectors of spores and seeds, box turtles are important as complementary dispersers and may serve an important role in maintaining community structure and dynamics. Unfortunately, turtle numbers have been declining over the last half-century (Stickel 1978, Williams and Parker 1987, Schwartz and Schwartz 1991, Dodd and Franz 1993). This decline may not only represent the potential loss of a species, but also the degeneration of a subtle plant-animal interaction in a system already challenged by habitat fragmentation.

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